Estuarine, Coastal and Shelf Science 309 (2024) 108959

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Mangrove forest ecological function is influenced by the environmental settings and the benthic fauna composition

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ARTICLE INFO

Keywords:
Benthic communities
Mangrove function
Environmental influence
Rhizophora stylosa
Regional variability

ABSTRACT

Benthic communities perform many important roles within mangrove ecosystems and are responsible for facilitating many of the functions attributed to mangrove forests. For instance, they are instrumental in mediating mangrove system productivity, and provide crucial food for juvenile nekton. Despite their importance, very few studies have investigated the benthic community of mangrove forests, and among those the results are inconsistent. This variability manifests in strong location effects, with low organism density and species richness in Indo-Pacific mangroves, compared to West Atlantic sites. These regional difference are confounded by differences in within-region environmental settings (e.g. rainfall, tidal range, spatial location along the coastal mosaic), and this complicates the development of a clear understanding of underlying consistencies. To assess the influence of contrasting environmental influences on the benthic community of mangrove forests we studied the benthic community of *Rhizophora stylosa* forests at two coastal estuaries and along the shores of two islands within a 75 km radius. The results showed that the community composition differed among settings, with several taxa only occurring at one of the two forests type. Furthermore, Peracarida, a common prey found in the gut of juvenile fish, was only found through the island forests, but never observed within the estuarine forests. This indicates that environmental setting can play a key role in determining the nature of mangrove benthic assemblages and their potential ecological roles. Consequently, caution is required when attributing the ecological roles of mangrove forests without accounting for changes in settings. Additionally, we only investigated a single mangrove species within the same climatic region, meaning that even greater variability is likely when the full range of mangrove types, conditions and areas are assessed. Understanding this variation is important because it implies that mangrove forest restoration projects are unlikely to achieve their desired outcomes unless setting-specific conditions are understood and taken into account.

1. Introduction

Mangroves support a spectrum of environmental functions and ecosystem services including coastal protection, carbon storage, and habitat and feeding areas for fish and invertebrates (Nagelkerken et al., 2008, Bryan-Brown et al., 2020). It is often argued that their value to fisheries species is one of the most prominent services that mangroves provide (Turner, 1977; López-Angarita et al., 2016). However, studies supporting the causal link between mangroves and fisheries productivity have generally been correlative and conducted at coarse spatial scales that encompass large expanses of coastline (100–1000 km) (Manson et al., 2005; Meynecke et al., 2008) and so do not unambiguously support the value of mangroves (Lee, 2004). In fact, the values often attributed to mangroves are a function of the complex interactions between mangroves and other components of the mosaic of coastal habitats (e.g. sandflats, seagrass) (Sheaves, 2009; Törnroos et al., 2013; Nagelkerken et al., 2015; Bradley et al., 2019). Nonetheless, mangrove forests receive special attention in relation to fisheries production because they are thought to provide nursery grounds for juvenile nekton (Robertson and Duke, 1987; Ley et al., 1994; Nagelkerken et al., 2001). However, the extent of this specific service is unclear because of a lack of knowledge of exactly how fish and mobile invertebrates (such as prawns and crabs) use mangroves.

Sheaves et al. (2016) determined that far fewer fish than expected access the mangrove forests of estuaries in northern Australia, with most activities concentrated along the forest edge. This edge-focused

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https://doi.org/10.1016/j.ecss.2024.108959
Received 2 April 2024; Received in revised form 20 August 2024; Accepted 13 September 2024

utilisation also occurs in quite different settings provided by Indo-Pacific mangrove-coral reef seascapes (Dubuc et al., 2019). This contrasts with studies in other parts of the world, in particular in the Caribbean where fish are observed accessing deeper into the forest (Nagelkerken et al., 2001). Similar variations in mangrove forest utilisation is evident among studies investigating mangrove benthic invertebrates. In fact, the diversity and species composition of benthic fauna in mangrove forests of North America and the Caribbean are widely different from those in the Indo-Pacific. For instance, organism density is often orders of magnitude higher in the Caribbean and America than in Indo-Pacific mangroves (Alongi, 1987, Sheridan, 1997; Sasekumar and Chong, 1998; Dittmann, 2000, 2001; Mattone and Sheaves, 2019**).** This disparity in benthic composition is likely to influence the details of the ecological roles that mangroves perform within their respective systems because the position of benthic invertebrates, at the bottom of the food webs, means they are directly and intimately involved in fundamental functions such as nutrient cycling and are key mediators of system productivity. Moreover, as a result of their position in food webs, benthic invertebrate communities often exert bottom-up control on species at higher trophic levels, so differences in benthic communities can influence the manner and extent of higher trophic group utilisation of an area (Grebmeier et al., 2006; Shurin et al., 2012; Davis et al., 2014).

Differences in the way marine organisms use mangrove habitats between the Indo-Pacific, the Caribbean and North America, may not simply be a function of geographic differences, but may also reflect site-specific characteristics in environmental settings. However, there is a tendency in the literature to consider mangrove forests as equivalent entities, regardless of mangrove species, morphology, location across the intertidal gradient, climate, tidal range or position in the landscape (e.g. estuarine, coastal, reef), and to generalize among geographic regions, without regard for, possibly marked, functional differences (Sheaves et al., 2020). For instance, mangroves in estuarine settings (where much of Australia's research has been conducted) are substantially influenced by sedimentation, freshwater fluxes and land run-off (Wolanski, 2014). In contrast, Caribbean studies have focused on mangroves in coastal-island, non-estuarine settings that occur in close proximity to other habitats such as coral reefs (Nagelkerken et al., 2001; Verweij et al., 2006). Variations in environmental settings are likely to influence the occurrence, distribution and composition of invertebrate fauna due to differences in the physical environment, water quality and the availability of recruits.

Variations in environmental settings are not necessarily a function of large geographic change but also occur at smaller scales. For instance, in northern Australia *Rhizophora stylosa*, one of the most common forest building mangroves, occurs in estuarine, coastal and island environment in the same coastal continuum. Over this range, they are exposed to substantial regional rainfall variation (700–4,000 mm mean annual rainfall), as well as different tidal ranges (ranging from >10 m to < 1 m), with consequent impacts on the timing and duration of forest inundation, and water quality (Baker et al., 2015)**.** If this diversity of settings is not taken into account the likelihood of misinterpretation of the ecological function of mangroves is obvious, as is the potential for this to lead to inappropriate management (Sheaves et al., 2020, 2021).

The potential range of unidentified variation in developing a spatially nuanced understanding of how different environmental settings affect ecological processes, is critical for science-informed management (Sheaves et al., 2021). Consequently, to improve the understanding of the potential for environmental settings to influence the functional role of mangrove forests we assessed differences in the composition of the invertebrate benthic communities of *Rhizophora stylosa* forests located in estuarine and non-estuarine settings within a single coastal region. Their location within a single coastal region means that these systems are influenced by similar climatic and environmental conditions. We focus on benthic invertebrates because their central importance to ecosystem processes means they are key indicators of ecological function, while their limited mobility and susceptibility to changes in environmental conditions, means that invertebrate assemblages are likely to reflect the long-term suitability of the system.

2. Materials and methods

2.1. Study sites

The study was conducted at four *Rhizophora stylosa* mangrove forests in north-eastern Australia (Fig. 1). Two field sites were located in estuarine settings: i) Blacksoil Creek (19.29806 S, 147.04083 E), ii) Cassady Creek (18.74166 S, 146.28916 E), and two along island shorelines: iii) Goold Island (18.1667 S, 146.1708 E), and iv) Orpheus Island (18.6112 S, 146.4919 E). All the forests are located within a 75 km radius and have similar meso-tidal regimes with a tidal range of about 3.5 m range.

The four mangrove forests are in zones where human impacts are limited to recreational fishing and tourism. Blacksoil Creek, Orpheus Island and Goold Island are situated within National Parks, thus direct human disturbance on the forest and the estuary are minimal. Cassady Creek is not part of a National Park, however, urban and agricultural development in the immediate vicinity is minimal.

Both island mangrove forests are in close proximity to coral reefs, and the coral influence was evident in the presence of coral rubble mixed through the sediment. The forest at Goold Island (Fig. 1A) is located on the southern side of the island, and is approximately 600 m in length, extending landward for about 140 m. The Orpheus Island forest (Fig. 1B) is located at the southern end of Pioneer Bay, is approximately 400 m in length and extends 60 m landwards. However, in the inner section of the forest (past 60 m), most mangroves display visible cyclone damage, with large amounts of rotting timber absent from other parts of the forest. Besides the damage in the inner section, the rest of the forest was in good health and the majority of the forest is composed of old well-established trees taller than 2 m. Both Island forests are mostly *Rhizopora stylosa* forest with sparse individual stems of *Aviecnnia marina.* On their landward sides both forests transition directly to terrestrial vegetation. The sediment on the surface is mud mixed with sand, with pieces of larger gravel and coral rubble mixed within.

The estuarine mangrove forests also comprised well-established trees taller than 2 m and both are located near the mouth of their respective estuaries. The Cassady Creek mangrove forest (Fig. 1C) was approximately 160m in length and extends 60 m landward before the mangrove species composition shifts from *Rhizophora stylosa* to *Ceriops* spp. As *Ceriops* occupy upper intertidal areas, this shift in mangrove species is an indication of an increase in elevation. The Blacksoil Creek mangrove forest (Fig. 1D) is approximately 600 m in length and extends landward for approximately 60 m, beyond which the mangrove composition shifts to low *Avicennia marina* and *Ceriops* spp. that gradually grade into salt marsh. Despite its proximity to the other sites, Blacksoil Creek has a substantially drier climate, receiving an average of 1100 mm per year, compared to the other sites that receive an average of ~2000 mm per Year).

2.2. Data collection

Sampling was conducted prior to the beginning of wet season rainfall; Cassady Creek in December 2014 and January 2015, and Blacksoil Creek in September and October 2014. The two island sites were sampled in September 2015. At each site, sampling occurred on the unvegetated tidal flat, 1 m seaward of the edge of the mangrove forest ('Tidal Flat'), and at two zones within the forest: 10 m ('Edge') and 40 m ('Inner'). On each sampling occasion a 10 cm diameter corer was used to sample sediment to approximately 20 cm depth. Six cores were collected per sampling zone. All samples were sieved though 0.5 mm mesh and animals identified to the lowest taxonomic level possible, usually Family or Order. During each sampling event an additional 5 cm diameter core sample was collected for sediment size and organic matter analysis. The

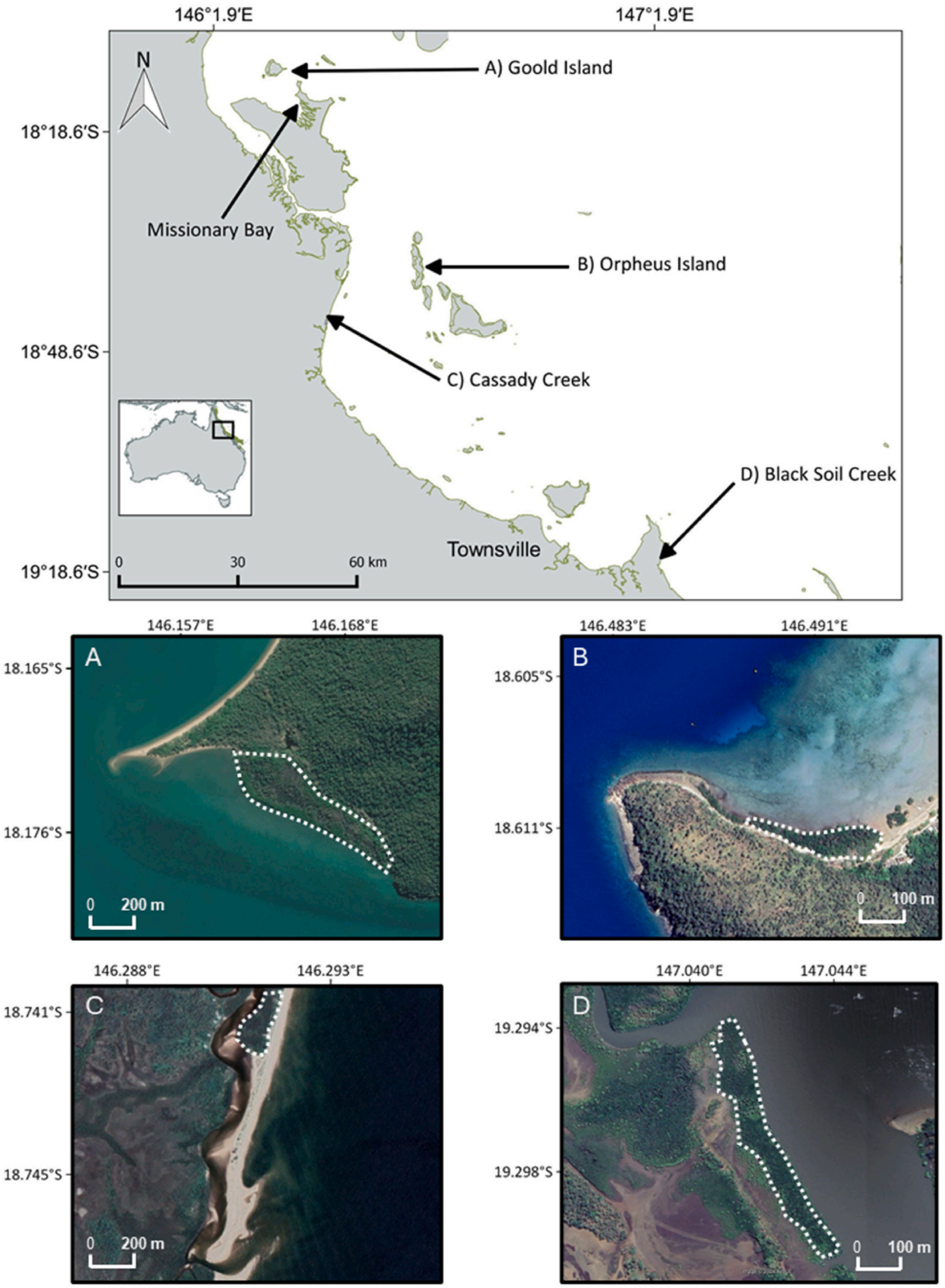

Fig. 1. Map of the study sites in north-eastern Australia: A) Goold Island, B) Orpheus Island, C) Cassady Creek, and D) Blacksoil Creek. Dashed white lineindicate the *Rhizophora* sp. forests where sampling occurred.

samples collected for sediment size analysis were first washed in freshwater to remove salt, and then dried at 105 °C. After the samples were dried, they were filtered using stacked sieves of 6 different mesh sizes (2 mm, 1 mm, 0.5 mm, 250 μm, 120 μm, 60 μm) and each fraction weighed. Organic content was estimated by loss through ignition where 5 g of dried sediment were placed in a muffle furnace at 500 °C for 8 h (Dean Jr, 1974). The difference in mass accounted for the organic content of the samples.

2.3. Data analysis

A principal component analysis (PCA) was conducted to determine similarities in sediment composition across sites and locations among the mangrove forests studied. The variables analysed were the sediment grain sizes (coarse sand = >1 mm, medium sand = 250 μm–1 mm, fine sand = 60 μm–250 μm, and mud = < 60 μm) and the organic matter content in the sediment. All the variables were normalized prior to analysis. Invertebrate abundance data were initially standardized by surface area and converted to density (individual per square m = ind/m^2). A non-metric Multidimensional Scaling Analysis (nMDS) of species composition was carried out using a Bray-Curtis dissimilarity matrix on log (x+1) transformed and then row standardized data. Prior to analysis the replicates were pooled together by site and location. Due to substantial patchiness of some organisms and the relative low sample density, species were grouped into broader taxonomic groups; this was considered acceptable because little information on spatial differences is lost using this procedure, while information on functional roles is retained (Chapman, 1998). Only taxa occurring in more than 5% of samples were included in the analyses. Due to their high mobility Brachyura were inconsistently represented in the core sampling, and therefore excluded from the analysis. Bubble plots of species densities were superimposed on the nMDS ordination to display the taxa with high correlation ($r > 0.5$) within the two-dimensional space.

3. Results

3.1. Sediment composition

The PCA for sediment grain size and organic matter revealed strong differentiation among the four sampling locations (Fig. 2). Coarse and medium sand characterised the Orpheus Island and most of Goold Island sites. Goold Island displayed substantial variability in sediment composition among the three tidal zones, with the majority of its 40 m sediment samples characterize by high organic matter content, probably reflecting the high level of rotting timber observed in the inner forest at Goold Island. The two estuarine mangrove sites (Blacksoil Creek and Cassady Creek) had overall much finer sediment composition. More specifically Blacksoil Creek sediment is characterized by fine sand and moderate mud and organic content while Cassady Creek vary between fine and moderate sand (Fig. 2). Cassady Creek also has a much wider variability in sediment composition across replicates, which is not observed at the other 3 locations, that have much tighter clusters among replicates (excluding the 40 m zone at Goold island). Interestingly, within each location, no clusters in sediment composition were observed based on the tidal zone (i.e. flat, edge, deep), with the sole exception of the higher organic matter content at the 40 m zone at Goold Island.

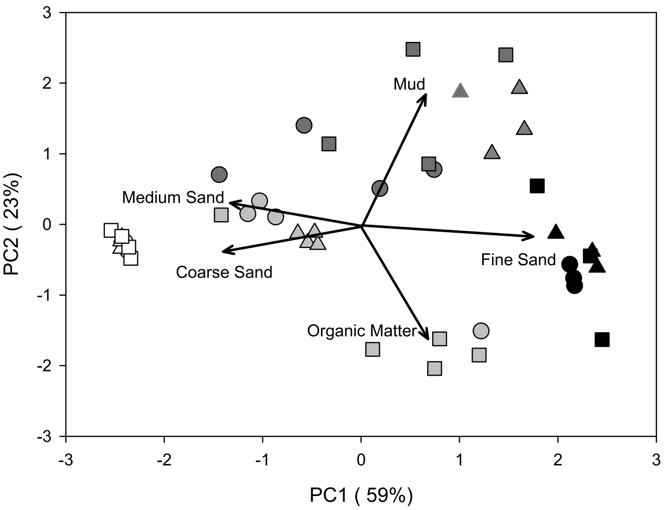

Fig. 2. Principal Component Analysis for sediment percent size and organic matter at the four study sites (Black = Blacksoil Creek, Dark Grey = Cassady Creek, Light Grey = Goold Island, Hollow = Orpheus Island) and three locations across the mangrove forest (Circle = Tidal Flat, Triangle = Edge, Square = Inner). The loading vectors of the sediment size (coarse sand = >1 mm, medium sand = 250 μm–1 mm, fine sand = 60 μm–250 μm, and mud = < 60 μm) and organic matter were superimposed on the ordination.

3.2. Invertebrate density

The tidal flats at Orpheus Island and Goold Island were characterized by a high density of benthic invertebrates, averaging 2462 ind./m^2 and 1847 ind./m^2 respectively. Interestingly, the samples collected inside the island forests had substantially lower animal density, averaging just 420 ind./m^2 at Orpheus Island and 588.5 ind./m^2 at Goold Island (Fig. 3). The two estuarine forests had similar animal densities both within and outside the forest averaging around 404.5 ind./m^2. Although the tidal flats on the islands had much higher animal densities compared to estuarine tidal flats, the mean animal densities inside the forests were comparable between the island and estuarine sites.

3.3. Species composition

The nMDS shows two clear clusters along the first dimension, with the island mangrove sites on one side (Orpheus Island and Goold Island) and the estuarine mangroves on the other (Cassady Creek and Blacksoil Creek) (Fig. 4 A). The differentiation in zones within location (i.e. tidal flat, edge and deep), is mostly visible along the second dimension, with the Cassady Creek having an anomalous position of the tidal flat zone, which is clustered closer to Blacksoil Creek, than the rest of the Cassady Creek points. The superimposed bubble plots indicate that most of the variability among the two clusters was due to higher presences of sipunculids and insects at the estuarine sites; taxa not observed at the two islands (Fig. 4B–D). Additionally, peracaridean crustaceans were observed throughout the forests at Orpheus and Goold Islands, but were only found outside the forest at the two estuarine locations (Fig. 4 C). Polychaetes were commonly found everywhere, however they occurred in higher densities at the island sites than the estuarine sites (Fig. 4 E).

3.4. Polychaete composition

The overall Polychaete composition at the four sites was mainly characterized by five families of polychaetes: Nereididae, Capitellidae, Glyceridae, Opheliidae and Spionidae (Fig. 5). However, the most noticeable feature was the extreme site-specificity in polychaete composition. Opheliidae only occurred at the two islands and were

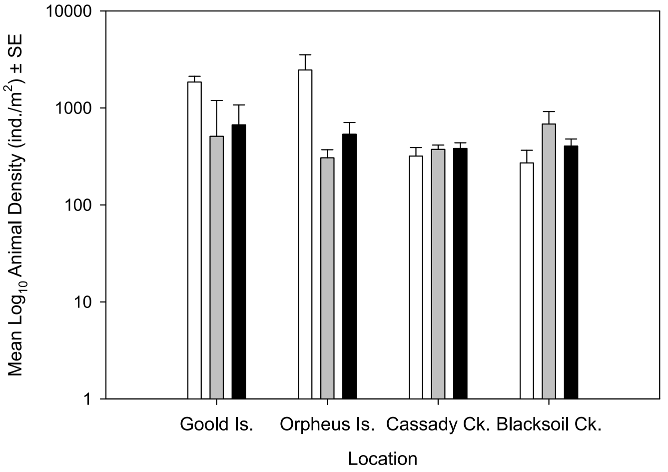

Fig. 3. Mean animal density across the forest gradient (White = Tidal Flat, Grey = Edge, and Black = Deep) at the four study locations (Goold Island, Orpheus Island, Cassady Creek, Blacksoil Creek).

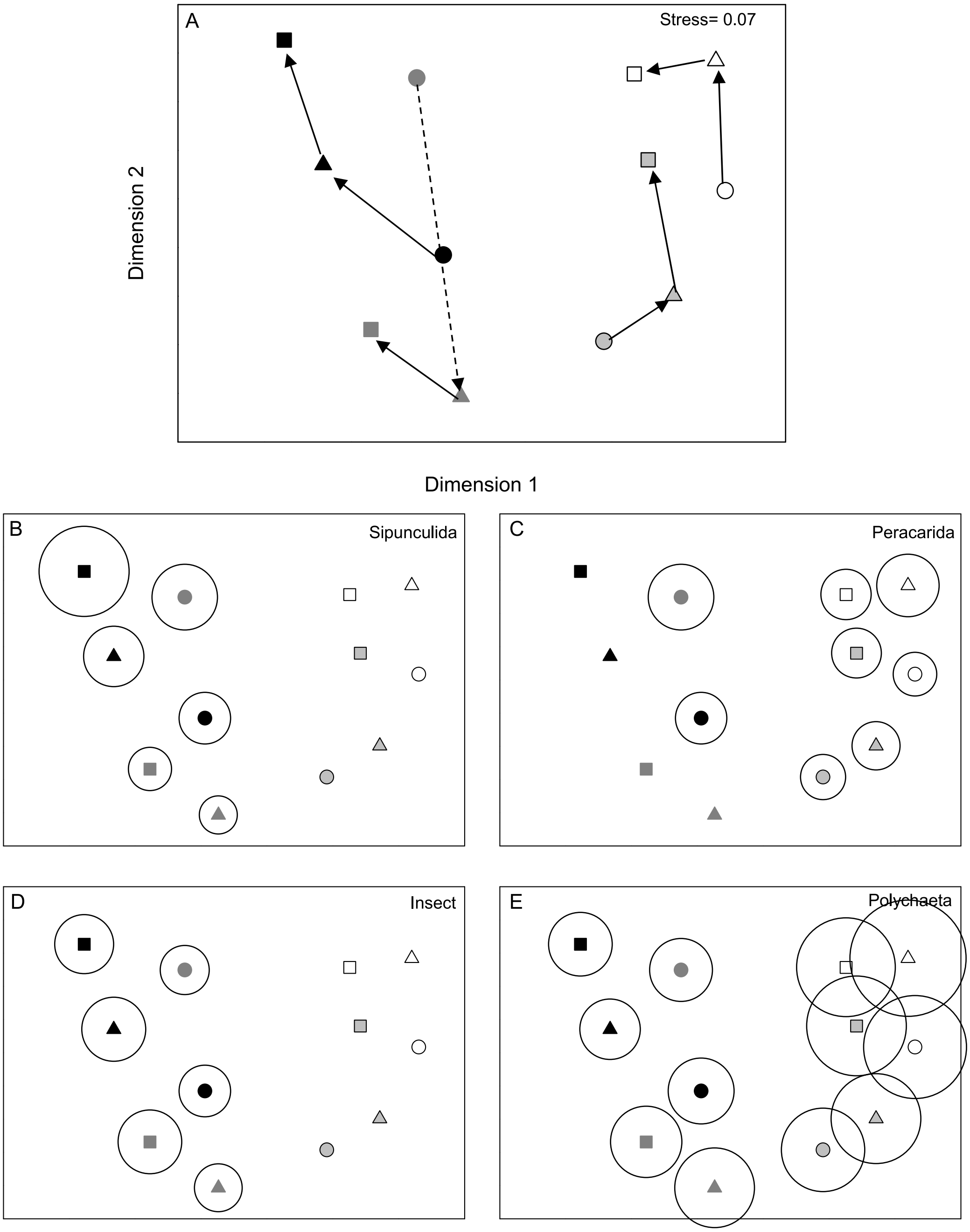

Fig. 4. nMDS ordination of benthic invertebrate species composition, constructed using a Bray-Curtis similarity matrix on Log (X+1) transformed and then raw standardized data, at the four sampling locations (Black = Blacksoil Creek, Dark Grey = Cassady Creek, Light Grey = Goold Island, White = Orpheus Island) across the three Zones (Circle = Tidal Flat, Triangle = Edge, Square = Deep). The Arrows are for illustration purpose only, and are designed to assist the sequencing pattern of zones within locations. Bubble plots of the most correlated species (B= Sipuncula, C= Peracarida, D = Insect, E = Polychaeta) are superimposed on the ordination, the size of the bubbles indicate the taxa density at each location.

particularly abundant at Orpheus Island, representing more than 50% of all polychaetes identified at that site, while Goold Island most abundant Family was Nereididae (58%). The two estuarine sites had the highest abundance of Capitellidae, with Cassady Creek almost exclusively composed of this Family (84%). Blacksoil Creek also displayed high density of Nereididae and Glyceridae, (38% and 18%, respectively).

4. Discussion

The composition of the benthic fauna of the *R. stylosa* forests sampled differed according to the environmental settings in which they were located, to the extent that estuarine and island mangrove forests were characterized by different taxonomic densities, and taxonomic mixes. Some of the changes in taxa are to be expected due to differences in salinity trends. For instance, Ophelidae polychaetes are strictly marine species (Rouse and Pleijel, 2001) and this explains why it was only observed at the two island locations, as the extensive seasonal fluctuations in salinity at the estuary sites would likely limit colonisation by this taxon. Other variations in community composition and dominant taxonomic groups are more difficult to explain. This is the case for Peracarids, as the taxa were absent within the estuarine forests, despite being found on the adjacent tidal flats.

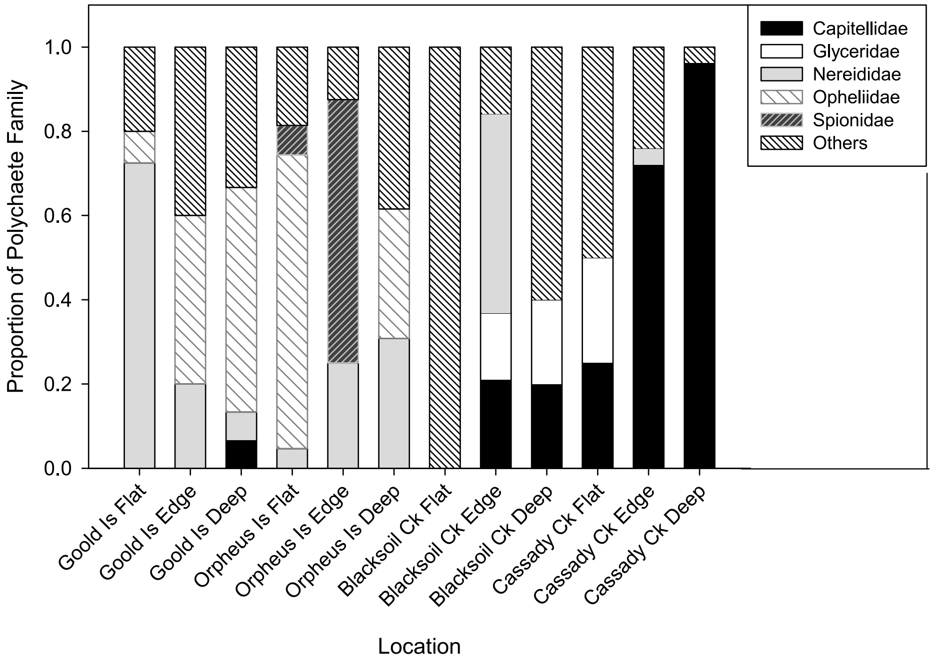

Fig. 5. Proportion of Polychaete Families density per location and zone.

Differences in sediment composition are also commonly associated with changes in fauna, and in the present study there was a major difference in sediment characteristics between the two environmental settings, with finer sediments in estuarine mangroves compared with coarser sand at the two island mangroves. The differences in sediment probably stem from the different hydrological dynamics, or sediment producing processes within the two systems. For example, island sites are often exposed to high wave energy, which prevents fine sediment from settling and results in coarser sand (Wright and Short, 1984). In contrast, estuarine sites are generally exposed to lower wave energy, leading to higher sedimentation rates and finer particles becoming trapped within the mangroves roots (Furukawa et al., 1997). This could explain some of the differences in taxonomic composition between the two mangrove settings. Interestingly, the absence of peracarideans within the two estuarine forest cannot be attributed to sediment characteristics alone, because no detectable variation in sediment was observed within the systems.

Mattone and Sheaves (2017) suggested that dissolved oxygen (DO) fluctuations could influence benthic fauna distribution in estuarine mangrove forests. It is possible that DO dynamics of island mangroves are different from estuarine forests. For example, The two Islands showned larger sediment size throughout the forest, and sediment coarseness can influence porosity, allowing oxygenated water to penetrate deeper (Wu and Wang, 2006). Less compact and coarse sediment would also enhance gas exchange, actively allowing more air to penetrate during tidal disconnection and reducing the repercussions of oxygen stripping activity performed by microbes. Additionally, the lower organic matter at the two island mangroves may further limit the impact of aquatic bacteria on DO (Streeter, 1931; Martin and Bella, 1971, Mattone et al., 2022). These variations may explain why DO sensitive organisms, such as peracarids, were observed in island mangroves and not within estuarine forests. On the other hand, taxa highly tolerant to low DO (e.g. Sipuncula, Capitellidae) are strongly represented in estuarine mangroves (Mattone and Sheaves, 2019), but their competitive advantage, might be reduced in systems with more stable physical conditions, allowing other species to become dominant (e.g. Nereididae). To further support this suggestion, during this study DO was measured at 5 min intervals over a sequence of 4 tides, and the preliminary results indicate that DO saturations at island sites is less depleted than at the estuarine sites (See supplementary material). More detailed investigations are needed to fully understand DO trends in the different settings, and the implications for different taxa.

Despite different taxonomic compositions between the two forests settings, overall animal densities within the mangroves were similar. However, there was a clear drop in density between the tidal flat and inside the forests at the island sites, suggesting that geographical setting influences patterns of invertebrate utilisation. There could be many, probably interactive, reasons for this sudden drop in abundance. For instance, microphytobenthos (MPB) productivity is lower within Rhizophora forests compared to the adjacent flats, despite having an overall higher biomass (Kwon et al., 2020). Therefore, lower quality food could hinder organism density and increase competition. However the higher biomass indicate that perhaps there is less grazing activity within the forest, and therefore many organisms could belong to different trophic identities (e.g. benthic carnivores), which would lead to increase predation and likely reduce the overall animal density.

The variability in benthic invertebrate composition among mangrove settings has considerable implications for mangrove ecology, because of the bottom-up pressures that benthos can exert on higher trophic levels (e.g. fish) (Grebmeier et al., 2006; Davis et al., 2014). As a result, the substantially different benthic assemblages found in the two environmental settings, are likely to influence the specific ecological role of mangrove forests and how nekton utilise their resources. For instance, Peracarida are believed to be an important source of food for juvenile nekton (Salini et al., 1990; Baker et al., 2005; Nanjo et al., 2008). Nonetheless this taxonomic group was never observed within forests in estuarine settings but only in island settings. This means that juvenile nekton would be faced with very different food resources depending on the mangrove settings. For instance, island settings, would still give opportunity to fish to feed on peracarids, while benefitting from other resources such as hydrological advantage and increase predator protection, at least in part explaining the different nekton occurring there (Dubuc et al., 2019). Other aspects likely to differentiate the ecology of the two mangrove system types, is the movement of nutrients, and nutrient cycling. The high content of organic matter in the estuarine forest and the presence of non-selective sediment feeder (e.g. Sipuncula), is likely to have different influences on nutrient cycling and export, compared to areas with lower organic content.

The implications of environmental settings go beyond the simple differentiation used here between estuary and island mangroves. For instance, Dittmann (2001) investigated the benthic fauna of mangrove forests at Missionary Bay (Hinchinbrook Island) adjacent to Goold Island (see Fig. 1), and reported a benthic faunal composition more similar to that at the estuarine mangroves sites, from the current study, than to Goold Island. In fact, the environmental setting of Missionary Bay more closely resembles that of estuarine systems (i.e. Blacksoil Creek and Cassady Creek), with relatively high sedimentation and freshwater than the nearby Goold Island, an so supports the idea that specific environmental settings plays a crucial role in determining the composition of mangrove benthic invertebrate assemblages and, by implication, their ecological roles.

Setting-specific and site-specific variations in invertebrate fauna seen in this study has implications for the way we understand the operation and functionality of these systems and relates directly to the substantial context dependence of mangrove fish (Bradley et al., 2024), and, in turn, to how we manage them. In particular, these results highlights the uncertainty of applying understanding gained from one location to another without prior validation (Sheaves et al., 2020). furthermore this study provides only a snapshot of the possible variability in in mangrove's function that can arinse from changes in settings. In fact, the research specifically assessed a single species of mangrove (*R. stylosa)* located in a very narrow coastal area exposed to similar environmental influences (e.g. tidal range, rainfall, temperature). However, Worldwide there are over 40 species of mangroves that span most of the tropics and sub-tropics, and occur along coasts with rainfall regimes ranging from arid to hyper wet, as well as across a diversity of geological and geomorphological settings. These substantial changes in mangrove floral composition and environmental conditions, likely result in further, yet-unidentified, variability in the ecological roles of mangrove forests. In fact, when we talk about 'mangrove forests' and 'mangrove forest function', we could be talking about vastly different things depending on location, setting and context.

This potential unexplored variation has substantial implications for the way we manage mangrove systems. In recent years, mangrove restoration and replantation projects have been implemented to offset the effects of human development and mangrove land reclamation (Ellison, 2000). However, measurement of restoration success is often simply based on vegetation characteristics (Lewis III 2005; Ruiz-Jaen and Mitchell Aide, 2005), without consideration of the impact on benthic fauna or the functional role of the forest (Sheaves et al., 2021). This means that, despite replication of floral characteristics, replanted forests might not provide the functions expected because of setting-specific environmental differences. Consequently, it is extremely important to expand our current understanding of how environmental settings influence the mangroves system functionality and move away from the current concept of "mangrove forests" as interchangeable units, regardless of their surroundings.

CRediT authorship contribution statement

Carlo Mattone: Writing – original draft, Formal analysis, Data curation, Conceptualization. **Marcus Sheaves:** Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Carlo Mattone reports financial support was provided by Commonwealth of Australia. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgment

This work was part of a Ph.D. project funded by an APAI scholarship (LP100100650) awarded to C.M.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108959.

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